THE ECOLOGICAL AND EVOLUTIONARY IMPORTANCE OF MATERNAL EFFECTS IN THE SEA

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Abstract   Maternal effects are non-genetic effects of the maternal phenotype or environment on the phenotype of offspring. Whilst maternal effects are now recognised as fundamentally important in terrestrial systems, they have received less recognition in the marine environment despite being remarkably common. The authors review the maternal effects literature and provide a simple framework for understanding maternal effects that increase offspring fitness (termed *anticipatory maternal effects*) and maternal effects that increase maternal fitness at the expense of offspring fitness (termed *selfish maternal effects*). The review then addresses various well-studied (offspring size effects, maternal care, oviposition effects) and poorly studied (manipulating offspring dispersal potential, toxicant resistance, sibling competition, mate choice) examples of maternal effects in the marine environment with a focus on marine invertebrates and fish. Offspring size effects are strong and pervasive in the marine environment but the sources and underlying causes of offspring size variation remain poorly understood. More generally, the authors suspect that changes in offspring phenotype are often adaptive maternal effects in response to environmental change. Maternal effects are of particular importance to marine systems because they not only form a link between the phenotypes of different generations, but the biphasic life cycle of most marine organisms suggests that maternal effects also link the phenotypes of populations.

Introduction

An organism's phenotype is the product of its genotype, the environment that the organism itself experiences and the environment or phenotype of its mother. This effect of the maternal environment or phenotype is termed a *maternal effect* and is one of the most important influences on offspring phenotype and performance (Wade 1998). For over 20 yr, maternal effects have been subject to intense interest in plants, insects and terrestrial vertebrates (Mousseau & Fox 1998a) but these pervasive and ubiquitous effects have received less attention in the marine environment. This review seeks to identify and explore maternal effects in the marine environment, calling on terrestrial examples where appropriate and highlighting the potential for maternal effects in a range of marine organisms.

For most organisms, maternal investment in each offspring exceeds paternal investment. Most multicellular organisms are anisogamous (produce gametes of different sizes): ova are large and sperm/pollen are small. The differential investment in gametes has led to mothers and fathers playing very different roles regarding their influence over the phenotype of their offspring. Whilst the contribution of fathers in most species is usually only genetic, mothers typically determine many aspects of the offspring phenotype. At the very least, mothers provide offspring with their nutritional requirements until they can feed for themselves but, in most organisms, mothers also determine the environment in which offspring develop and the environment in which they are released or become

independent. This close association between offspring and mother has led to the recognition that maternal effects are the most important determinant of an offspring's initial phenotype (Wade 1998). Whilst maternal effects were originally considered troublesome sources of variation in quantitative genetic studies (Falconer 1981), evolutionary biologists now recognise that maternal effects can influence evolutionary trajectories, speciation rates (Wade 1998) and oscillations in mean phenotype (Mousseau & Fox 1998a). Simultaneously, it has become clear that the role of maternal effects in ecology cannot be ignored. Maternal effects can generate population cycles (Ginzburg 1998), buffer phenotypic variation in relation to environmental change and link the phenotypes of different populations/generations (Plaistow et al. 2006). Accordingly, the number of studies examining maternal effects has increased dramatically (Figure 1). Classic examples of maternal effects in terrestrial systems include offspring provisioning (e.g., offspring size), brood protection and oviposition site, but also include less-obvious effects such as the manipulation of gene expression in offspring, offspring dispersal profiles, immune responses, resistance to toxicants, offspring competition and sex determination. Thus maternal effects encompass a range of different influences on the phenotype of offspring and these effects have become a major field of study in evolutionary ecology across a range of taxa. In marine systems, however, maternal effects have received far less attention.

The most striking maternal effect is the effect of offspring size (or provisioning) on offspring performance. Juveniles with identical genetic backgrounds can differ dramatically in their chances of survival and reproduction due to differences in the amount of resources they receive from their mothers. Accordingly, there have been a number of reviews of offspring size effects in marine invertebrates and fish (see Emlet et al. 1987, Chambers & Leggett 1996, Chambers 1997, Ramirez-Llodra 2002, Marshall & Keough in 2008a). However, maternal effects as a whole have received very little consideration in marine systems and many types of maternal effects have not been considered at all. This seems remarkable given that the supply of new individuals into marine populations is recognised as an important driver of marine population dynamics (Underwood & Keough 2001). Given that maternal effects can strongly affect the performance of offspring, one can easily imagine that maternal effects play an important role in marine systems but these effects are largely unexplored, or more importantly, unrecognised.

When the marine literature is examined, it quickly becomes apparent that maternal effects are important and prevalent; however, they are sometimes not recognised for what they are.
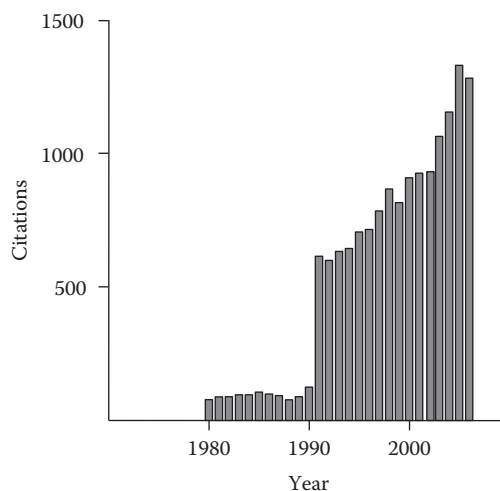

Figure 1 Number of citations of studies examining maternal effects since 1980. Data produced from entering "maternal effects" as a search topic into ISI Web of Science.

Consequently, in many studies where authors find that the maternal phenotype affects the phenotype of the offspring, they have been forced to 'reinvent the wheel' with regard to providing ecological and evolutionary implications of the observed effects. Furthermore, in the absence of a broader maternal effects framework, it can be difficult to reconcile seemingly conflicting findings. For example, why does maternal nutritional stress result in a decrease in offspring size in some species whilst it induces an increase in offspring size in others? The present authors believe that many of these seemingly disparate phenomena can be unified under the single theme of maternal effects and that an understanding of these effects will be facilitated by viewing them in such a framework. It is also hoped that this will guide future research such that previously unconsidered forms of maternal effects may well be common in the marine environment. The goals for this review, therefore, are to

1. Provide an overview of current maternal effects theory and develop a general framework for viewing maternal effects in the marine environment.
2. Briefly review the incidence and types of maternal effects in terrestrial systems to provide a guide to likely maternal effects in the marine environment.
3. Review the types and sources of maternal effects in marine organisms.
4. Highlight the potential importance of maternal effects for the ecology and evolution of marine populations.
5. Provide some suggestions for new approaches and directions for the study of maternal effects in the marine environment.

The first goal is to familiarise workers in marine systems with a field of study that is becoming increasingly sophisticated in terrestrial systems. It is also hoped that this section provides a new framework for interpreting maternal effects in an ecological and evolutionary context. The second goal is to illustrate the range of maternal effects in well-studied, terrestrial organisms as a means of indicating which organisms/stages in marine systems are also likely to exhibit maternal effects. The third goal is to review the available literature on maternal effects in marine systems and the authors have striven to also find those studies that may not have been interpreted as maternal effects by the original authors but may be viewed as such. The fourth goal is to highlight the particular importance of maternal effects for marine systems. The implications of maternal effects for marine populations specifically have been overlooked by most general considerations but in this review an attempt is made to illustrate why maternal effects are likely to be important in the dynamics and evolutionary trajectories of marine populations. The final goal is to identify the significant gaps in our understanding of maternal effects in marine systems and it is the authors' desire to encourage more research into what is believed will be fruitful lines of further research.

An introduction to maternal effects

In this section, the authors aim to provide the fundamentals of maternal effects for those who have not previously considered maternal effects in an ecological and evolutionary framework. First, a framework is provided for viewing and discussing maternal effects and to provide some means of classifying different types of maternal effects. Then an overview of maternal effects in terrestrial systems is given as a means of both familiarising the reader with common maternal effects and illustrating the breadth and sophistication of the field outside of the marine environment.

Maternal effects: definitions and usage

Numerous excellent reviews have provided a general history of maternal effects and the reader is directed to these for a historical overview of the study of maternal effects (see Roach & Wulff 1987,

Mousseau & Dingle 1991, Mousseau & Fox 1998b,c). Similarly, there are many different definitions of maternal effects and it seems that each new review of the topic provides a different definition. This reflects the nebulous nature of maternal effects more than any imprecision or redundancy by previous authors: whilst some phenomena (such as varying energetic investment in offspring) are clearly maternal effects, others seem harder to classify. For the purposes of this review, Elizabeth Lacey's definition of maternal effects is the most useful; she defines a parental effect as 'any [maternal] influence on offspring phenotype that cannot be attributed solely to offspring genotype, to the direct action of the [non-maternal] components of the offspring's environment, or to their combination' (1998, p. 56; note that the present authors have slightly modified this definition [material in square brackets] to exclude paternal effects as there are too few data to speculate regarding paternal effects in marine systems). The most difficult part of this definition is determining what the 'non-parental components' of the offspring's environment actually are. If the mother determines the site of offspring release, then many aspects of the offspring's external environment will still be influenced by mothers. This matter is discussed further in this review. Nevertheless, this definition is probably the most comprehensive whilst still excluding some ambiguous issues such as extranuclear inheritance (for a comprehensive discussion of the nomenclature of maternal effects, see Lacey 1998).

Maternal effects can take a variety of forms and can dramatically increase or decrease the fitness of their offspring. Maternal effects can act as a buffer against environmental variation, enhancing offspring fitness. However, maternal effects can also act as a conduit by which environmental variation in the maternal generation can influence the phenotype of offspring. Thus, before maternal effects in the marine environment are explored, it is necessary to consider ways in which to classify and group maternal effects. Wade (1998) divided maternal effects into stages (prezygotic, postzygotic-prenatal and postzygotic-postnatal) according to when they manifest themselves. Lacey (1998) considered the three general genetic mechanisms by which maternal effects can act to affect offspring phenotype. Whilst these classifications are useful for different aspects of the study of maternal effects, for the purposes of this review an outcome-based approach is proposed. By focusing on the consequences of different maternal effects, it is hoped that their evolutionary and demographic implications will be made clearer.

Maternal effects can sometimes act to increase offspring fitness in the subsequent generation and are therefore sometimes considered 'adaptive maternal effects' (Bernardo 1996a,b, Mousseau & Fox 1998b, Agrawal 2001). However, several authors have suggested caution with regard to viewing maternal effects as adaptive and indeed there are numerous examples of maternal effects *decreasing* offspring fitness (Bayne et al. 1975, Bernardo 1996b, Rossiter 1996). Thus there has been an interesting debate on the adaptive significance of maternal effects (Heath & Blouw 1998). Why do maternal effects sometimes act to increase offspring fitness but other times decrease maternal fitness?

Importantly, maternal effects are typically classed as 'adaptive' only when they increase the fitness of their offspring (Mousseau & Fox 1998a,b). However, maternal effects that decrease offspring fitness may still increase the fitness of the mother. For example, bryozoan colonies that suffer a predation event redirect their resources away from their offspring, temporarily producing offspring that have lower chances of survival (Marshall & Keough 2004a). Whilst a reduction in offspring size reduces the fitness of *offspring*, this maternal effect may still increase *maternal* fitness because it provides mothers with more resources for recovering from the predation event (Marshall & Keough 2004a). It may thus be misleading to regard maternal effects as adaptive on the basis of their effects on offspring alone.

It is important to note that whilst it may seem counterintuitive, the fitness of mothers and offspring are not necessarily correlated. To explain, maternal effects such as offspring size can be regarded as a phenotype that both the mother and offspring 'share' in that variation in the phenotype will affect the fitness of both mothers and offspring (Bernardo 1996b). However, whilst the fitness of both mother and offspring are affected, selection will act on the maternal effect to maximise

maternal fitness *only* (Smith & Fretwell 1974, Bernardo 1996a). The simplest way to understand why selection maximises maternal, rather than offspring, fitness is to consider the alternative. If selection acted to maximise offspring fitness, then mothers would produce one large, 'perfectly' resourced offspring that consumed all of her resources such that she died following reproduction. In reality, mothers typically produce many offspring that each have lower fitness but the fecundity benefits are such that maternal fitness is higher overall (Einum & Fleming 2000a). Thus mothers and offspring are in conflict with regard to the level of maternal investment that benefits each party and their respective interests will only sometimes be aligned (whether that be provisioning, brood protection, oviposition site, etc.; Trivers 1974). Thus maternal effects may still be adaptive (for mothers) even if they result in a decrease in average offspring fitness. Accordingly, it is suggested that maternal effects be classed according to their consequences for offspring and suggest the terms *anticipatory maternal effects* (AMEs) and *selfish maternal effects* (SMEs) to describe the two broad classes of maternal effects (Marshall & Uller 2007).

Anticipatory maternal effects are defined here as manipulations of offspring phenotype that act to increase maternal fitness by increasing fitness of individual offspring. Such examples are common in the terrestrial literature and are examined in more detail below. Importantly, mothers must be able to 'anticipate' (or at least influence; Einum & Fleming 2002) the natal environment in order for mothers to produce offspring with the appropriate phenotype. Note that the present authors recognise that this 'anticipation' does not involve a conscious prediction regarding the offspring environment by which mothers 'choose' the appropriate phenotype of their offspring; rather the word 'anticipate' is here used as a convenient shorthand to denote that selection should favour mothers that produce offspring of a certain phenotype when the maternal environment is a good predictor of the environment the offspring will encounter.

Selfish maternal effects are defined here as manipulations of the offspring phenotype that act to increase maternal fitness by decreasing offspring fitness. When mothers are under nutritional, competition or pollution stress, they sometimes reduce the mean quality of their offspring (George et al. 1991, Cox & Ward 2002, Marshall & Keough 2004a, McCormick 2006). These effects may be regarded as 'selfish' in that mothers are effectively sacrificing current offspring performance for their own survival or for increased fecundity. Importantly, redirecting resources away from offspring will only benefit mothers if they have a good chance of using those resources to increase their overall reproductive success.

Whilst decreasing the mean quality/phenotype of offspring in response to environmental change is likely to be common, it is not the only way in which mothers may increase their overall fitness at the expense of offspring in the current round of reproduction. When the environment varies unpredictably or there is uncertainty regarding the habitat to which offspring will disperse, selection may favour mothers to produce a range of offspring phenotypes (phenotypic bet hedging; Seger & Brockman 1987). For example, if mothers cannot 'predict' the habitat or competitive environment of their offspring, mothers that produce a range of offspring sizes should be favoured (Capinera 1979, Crump 1981, McGinley et al. 1987, Geritz 1995, Dziminski & Alford 2005). Mothers can also manipulate the dispersal profiles of their offspring and in a range of taxa, mothers produce offspring with a range of dispersal phenotypes so as to 'spread their risk' regarding the colonisation of new habitats (Strathmann 1974, Zera & Denno 1997, Krug & Zimmer 2000, Krug 2001, Toonen & Pawlik 2001). Thus it is suggested here that there are two broad classes of maternal effects: AMEs, which act to increase offspring fitness, and SMEs, which act to decrease offspring fitness. Throughout this review, different maternal effects are described using this terminology where possible. It is hoped that the use of this terminology emphasises that maternal effects generally are unlikely to be simple environmental 'by-products' that are impervious to selection and, at the very least, should be scrutinised in a selection framework.

Examples of maternal effects in terrestrial systems

Maternal effects have been the object of study in terrestrial systems for almost 100 yr (reviewed in Roach & Wulff 1987). The goal in this section is to use this literature to highlight the diversity of potential maternal effects and indicate how similar analogues may occur in the marine environment. Simultaneously, the reader is made aware from discussion of some well-studied and classic examples of maternal effects, and of the general types of maternal effects that have been the object of study in other systems, in the hope that clear parallels can be seen in marine systems.

Plants and insects are among the best-studied groups and there is a rich and sophisticated literature on maternal effects in these two groups (Wulff 1986a,b, Mousseau & Dingle 1991, Bernardo 1996a,b, Mousseau & Fox 1998b). Maternal effects in these groups range from simple effects such as propagule size effects (for a recent review, see Bernardo 1996a) through to more dramatic manipulations of offspring phenotype, such as predation resistance. It is noted that there are a number of maternal effects (such as post-hatching parental care in birds; Stenning 1996) that are common in terrestrial systems but herein the focus is on maternal effects that are likely to have clear analogues in the marine environment.

Offspring provisioning

Some of the best examples of AMEs involve the manipulation of offspring size by mothers. In an elegant series of experiments on the seed beetle *Stator limbatus*, Fox et al. (1997) showed that mothers produce larger eggs when they lay their offspring on thick-coated (well-defended) seeds. These extra resources better enable offspring to bore through the thick seed coats. A similar effect is observed in the heteropteran *Adomerus triguttulus*; when mothers are presented with poor-quality seeds, they increase the ratio of trophic eggs to viable eggs that they lay (Kudo & Nakahira 2005). Trophic eggs are non-viable eggs upon which offspring can feed (analogous to nurse eggs in marine gastropods) and represent an alternative food source for the offspring under poor food conditions.

In plants, there is a rich literature on seed size effects and the reader is directed to these specific reviews (e.g., Coomes & Grubb 2003, Moles & Westoby 2003, Moles et al. 2005). Interestingly, most seed size considerations focus on among-species effects (reviews above) but nevertheless, there is also an extensive literature on within-species effects and some of the best known and most interesting examples of offspring size as a maternal effect come from plant studies (Stanton 1984, 1985, Galloway 1995, 2001a, Bernardo 1996a). Overall, plant mothers can be remarkably sophisticated regarding offspring provisioning, increasing the size of seeds in response to decreases in environmental quality such that offspring have a greater chance of subsequent survival (Agrawal 2001). Importantly, there can be conflicting selection on offspring size in plants. For example, increases in offspring size can positively influence competitive ability but can also increase the risk of predation (Gomez 2004). It is suggested that the general experimental approaches in these studies could serve as excellent models for studies of offspring size effects in sessile marine organisms.

Studies of offspring provisioning in freshwater fish are relatively more common than marine studies and one of the first examples of offspring size effects comes from a study on the brown trout, *Salmo trutta* (Bagenal 1969). More recently, Einum and Fleming, in a number of excellent papers, show that offspring size effects can be strong, pervasive and highly context dependent in freshwater fish (Einum & Fleming 1999, 2000b, Einum et al. 2002, Einum 2003).

Terrestrial studies of offspring size as a maternal effect suggest that some generalisations can be made. Generally, benign environments will select for a decrease in offspring size (Einum & Fleming 1999, Fox 2000). Accordingly, offspring size effects should be examined under field conditions whenever possible. However, whilst initial increases in environmental 'harshness' probably result in selection for increasing offspring size, very harsh environments may not select for increased offspring size (Brockelman 1975). The present authors suggest that, rather than classifying

environments as 'harsh' or 'benign', future research should focus directly on the relationship between offspring size and performance as, ultimately, this will be the most important determinant of the benefits of increasing or decreasing offspring size (Smith & Fretwell 1974, Parker & Begon 1986, McGinley et al. 1987, Bernardo 1996a).

Dispersal

The manipulation of offspring dispersal potential is one of the most interesting and dramatic types of a maternal effect in terrestrial systems (Mousseau & Dingle 1991, Zera & Denno 1997, Mandak & Pysek 1999, Parciak 2002). In a classic example, when pea aphid (*Acyrthosiphon pisum*) mothers experience 'crowding' (high intraspecific competition), they produce more dispersive (winged) offspring that can escape the poor-quality environment (Sutherland 1969). Similarly in reptiles, mothers can manipulate offspring hormone levels to affect their tendency to disperse (Shine & Downes 1999, De Fraipont et al. 2000, Olsson et al. 2002).

Offspring dormancy

Another well-studied aspect of maternal effects relates to offspring diapause in insects. Photoperiod is the most widely studied environmental effect on diapause, but others include temperature (and interaction with photoperiod), maternal age, host availability, maternal starvation, and geographic location (Mousseau & Dingle 1991). In an analogous example in plants, maternal nutritional history can also affect the timing of germination (Galloway 2001b).

Offspring defences

Some maternal effects can be remarkably sophisticated and these effects can act to buffer offspring from negative changes in their environment. In terrestrial plants and freshwater invertebrates, mothers that experience predation (or cues for predation) can produce predation-resistant offspring, inducing permanent phenotypic changes in their offspring (Agrawal et al. 1999). For some terrestrial invertebrates and freshwater fish, mothers that experience heavy metal stress increase the pollution resistance of their offspring (Munkittrick & Dixon 1988, Vidal & Horne 2003), possibly by increasing the level of metallothionen-producing RNA in their eggs (Lin et al. 2000) or increasing offspring size (Hendrickx et al. 2003). Similarly, maternal effects can act to increase offspring resistance to toxins contained in their food (Gustafsson et al. 2005). Interestingly, in the cladoceran *Daphnia magna*, mothers kept in poor food environments produce offspring that are more resistant to bacterial infection (Mitchell & Read 2005).

Oviposition site

The location that mothers choose to lay their eggs will dramatically influence the subsequent survival/performance of their offspring and the most common examples of these effects are in phytophageous insects (Mousseau & Dingle 1991, Sadeghi & Gilbert 2000, Monks & Kelly 2003). Importantly, maternal age and the number of eggs that she is carrying (her 'egg load') can strongly affect the strength of preference in mothers whereby older, or high-egg-load mothers will accept lower-ranked (and thus lower-quality) plants (Singer et al. 1992, Fletcher et al. 1994, Sadeghi & Gilbert 2000, West & Cunningham 2002, Javois & Tammaru 2004). Thus the maternal environment/experience can strongly influence offspring performance by determining the local environment of the offspring in species for which eggs are bound to one site for some period. Whether similar effects occur in marine organisms is an unexplored but intriguing possibility with initial studies suggesting such effects are likely (von Dassow & Strathmann 2005). Oviposition as a maternal effect is, of course, not restricted to phytophageous insects: beetle mothers also avoid ponds that contain predators (Brodin et al. 2006) and later in this review, the various effects of oviposition in amphibians are highlighted.

AMEs versus SMEs

Most of the examples cited above represent AMEs and whilst such examples are common, there are equally numerous examples of SMEs in terrestrial organisms and the authors do not wish to mislead that maternal effects are commonly AMEs in terrestrial systems. For example, as phytophageous mothers age or accumulate eggs, they tend to accept lower-quality plant hosts on which to lay their offspring (Singer et al. 1992, Fletcher et al. 1994, Sadeghi & Gilbert 2000, Javois & Tammaru 2004). Similarly, in five species of acanthosomatid stink bugs mothers tend to lay smaller (poorer-quality) eggs on the periphery of their clutches because these eggs are more likely to experience mortality due to predation (Kudo 2001). Numerous abiotic factors negatively affect seed size in plants and offspring size in animals and the reader is directed to a number of excellent reviews on this topic (Williams 1994, Bernardo 1996b, Rossiter 1996). Maternal exposure to toxicants can have strong, negative effects on offspring fitness with numerous human examples (Gallagher et al. 1998, Sram et al. 2005). Finally, another maternal effect that has received less attention is the influence of maternal fecundity on offspring performance as mediated through sibling competition (Beckerman et al. 2006). If offspring dispersal is poor, offspring from highly fecund mothers will experience higher levels of intraspecific competition (and lower performance) than offspring from less-fecund mothers (Klug et al. 2006).

Overall, maternal effects can dramatically change the performance of offspring and there are a number of clear analogues between the effects observed in terrestrial systems and those that may occur in marine systems. Mothers have the potential to affect the size, dispersal potential, point of release and general phenotype of their offspring in a range of marine organisms, but many of these effects have received scant attention in the marine literature.

Types and sources of marine maternal effects

This section deals with the types of maternal effects present (or likely to be present) in the marine environment and how they have an impact on offspring fitness and population dynamics. For some effects there is excellent evidence for their importance and prevalence (e.g., offspring size effects) but for others, evidence is limited (e.g., oviposition effects). Nevertheless, terrestrial studies suggest that these less-studied effects are likely to be of similar importance in the marine environment; they have simply been overlooked thus far. For maternal effects for which evidence is limited, attention is drawn to their potential importance and to avenues of investigation that may be valuable. The scope of this review is limited to marine invertebrates and fish despite the fact that maternal effects are likely to occur to some degree in all marine organisms. Literature on maternal effects in marine reptiles such as turtles is therefore excluded, but it is noted that offspring phenotype (including sex) can be affected by maternal nest site choice in this group (Godley et al. 2002, Burgess et al. 2006). Similarly, discussion of maternal effects in marine birds is excluded as there is too little space to cover this rich literature. Discussion of maternal effects in marine algae is also excluded, in this case because of the scarcity of appropriate studies.

Maternal investment

Maternal investment may be defined as an association between a mother and her offspring, before or after fertilisation, that carries an energetic or fitness cost for the mother and a fitness benefit for the offspring (Clutton-Brock 1991). Benefits of parental investment for offspring include reducing the risk of predation/starvation, lowering the negative effects of adverse environmental conditions, or increasing the rate of development. However, providing care may incur costs to parents such as decreased parental survival, decreased mating opportunities, or reduced number of offspring (Sargent 1997). Hence, parents may increase their reproductive output through either continued

investment into present progeny (thereby increasing offspring survivorship and fertility; i.e., AMEs) or investment into expected future progeny (through increased adult survivorship and fertility; i.e., SMEs). Therefore, any parent that continues to invest in its offspring does so at the expense of its potential future reproduction and hence should invest according to the value of its current brood relative to that of its own expected future reproduction (Williams 1966).

Offspring provisioning

Offspring provisioning (which, for the purposes of this review, encompasses propagule size and subsequent nutritional input from the mother) is one of the most obvious types of maternal effects and can have far-reaching consequences for the performance and phenotypes of offspring. In every taxon that has been studied, offspring size affects many important components of offspring fitness (Bernardo 1996a) and the marine environment is no exception. Several reviews have examined the role of offspring size on subsequent performance in marine fish (Kamler 1992, Chambers & Leggett 1996, Chambers 1997) and invertebrates (Marshall & Keough 2008a) and the reader is invited to explore these for an in-depth review of causes and the consequences of offspring size variation in these groups. The present goal, therefore, is not to retrace old ground but to briefly summarise the state of knowledge of these effects and highlight their importance. The factors that affect the degree to which mothers provision their offspring (i.e., the sources of this maternal effect) are then addressed. Note that because of the differences in life-history stages among marine invertebrates and fish, these two groups are considered separately.

Effects of offspring provisioning on offspring performance: marine invertebrates The study of offspring size effects in marine invertebrates has a long history. Thorson (1950) was one of the first to seek to understand the broad interspecific and geographical patterns in offspring size in marine invertebrates. Whilst the interspecific variation in offspring size is impressive in marine invertebrates, here the focus is on intraspecific variation and effects of offspring size. Offspring size has pervasive effects on subsequent performance in marine invertebrates, affecting every life-history stage with potentially dramatic consequences for fitness.

In broadcast spawners (i.e., those that shed eggs and sperm into the surrounding medium), larger eggs are larger targets for sperm and are therefore more likely to be fertilised at low concentrations of sperm (Levitan 1996a). However, at higher sperm concentrations, larger eggs are more likely to suffer polyspermy (Marshall et al. 2002), a fatal condition in marine invertebrates. These effects of egg size on fertilisation kinetics suggest that the fitness return of producing offspring of any one size will strongly depend on the local sperm environment in broadcast spawners. Levitan (2002) even suggests that differences in the size of eggs produced by three sea-urchin species are due to differences in the average sperm environment: species with an increased risk of sperm limitation produce larger eggs than species for which sperm limitation is less likely. On ecological timescales, whether mothers adaptively adjust the size of their eggs according to local sperm conditions remains unclear. Certainly the threat of fertilisation failure (either through sperm limitation or polyspermy) due to producing eggs that are the 'wrong' size for the local sperm environment must represent a strong, proximal selection pressure and previous studies suggest that broadcast spawners can 'detect' the presence of other individuals during gametogenesis (Hamel & Mercier 1996). Nevertheless, given the pervasive effects of offspring size in later life-history stages, the present authors wonder whether mothers can adjust egg sizes for one stage irrespective of downstream effects and still gain a fitness benefit. An intriguing experiment would be to manipulate the density of a species with external fertilisation and determine if the species adjusts the size of its eggs accordingly.

In species with non-feeding larvae, offspring size affects a number of elements of the pelagic period. Egg size affects development time in broadcast spawners, with larvae from larger eggs generally taking longer to become competent to settle than larvae from smaller eggs (Marshall

& Bolton 2007; but see Marshall et al. 2000). Larval size can determine the maximum longevity of coral larvae (Isomura & Nishimura 2001), with larger larvae surviving for longer periods than smaller larvae. Similarly, larval settlement behaviour depends on larval size, with larger larvae remaining 'choosy' regarding settlement cues for longer than smaller larvae (Marshall & Keough 2003a). In both the laboratory and the field, smaller larvae accept poor-quality settlement cues sooner than larger larvae in three species of colonial invertebrate (Marshall & Keough 2003a). Presumably, the effects of offspring size on larval longevity and settlement behaviour are mediated via energetics: larger larvae have more resources and can better 'afford' to engage in costly swimming (Hoegh-Guldberg & Emlet 1997, Bennett & Marshall 2005) than smaller larvae. The effects of offspring size on the timing of the onset of competence to metamorphose, longevity and the onset of indiscriminate settlement all suggest that there is potential for marine invertebrate mothers with non-feeding larvae to manipulate the dispersal (both the minimum and maximum) of their offspring. In terrestrial systems, mothers manipulate the dispersal potential of their offspring according to local conditions in order to maximise their own fitness (aphids: Sutherland 1969, plants: Donohue 1998, lizards: De Fraipont et al. 2000). Whilst this idea has not been explored specifically in marine invertebrates, Krug (1998) showed that mothers in poor-quality environments produced more dispersive offspring than mothers in higher-quality environments for the sacoglossan *Alderia modesta*. Whether or not mothers change the size (and thus dispersal properties) of their offspring according to local conditions remains an intriguing, but largely untested, possibility. Nevertheless, any environmental factors that change the size of offspring within a population will consequently alter the dispersal profile of larvae in that population and this has interesting implications for the dynamics of that population (Fowler 2005). For example, a stress that reduces mean offspring size will result in fewer larvae being likely to 'escape' that population.

In species with feeding larvae, offspring size effects (and maternal effects generally) have been viewed as weaker because maternal provisioning provides only a small proportion of total resources upon settlement (Marshall & Keough 2008a). Nevertheless, egg/larval size affects larval feeding ability, the length of the feeding period and post-metamorphic size in echinoids with feeding larvae (Hart 1995, McEdward 1996, Allen et al. 2006) and it seems likely that larger eggs will be favoured when planktonic food is scarce (Allen et al. 2006). Again, one might expect mothers to adaptively react to local planktonic food concentrations by producing larger or smaller eggs, especially in species that are filter-feeders as adults (and can therefore better assess the conditions their offspring will encounter) but this has not been tested.

The effects of offspring size cross the metamorphic boundary, affecting post-metamorphic performance in a range of marine invertebrates with non-feeding larvae or direct development (no larval stage). In colonial marine invertebrates, larval size affects survival, growth (Marshall et al. 2003, Marshall & Keough 2004b, 2005, Marshall et al. 2006) and even reproduction and second-generation offspring quality (Marshall et al. 2003) in the field. In unitary (non-colonial) organisms, Ito (1997) found that offspring from larger eggs in the opisthobranch *Haloa japonica* were more resistant to starvation than offspring from smaller eggs and Marshall & Keough (2003b) found that larger *Ciona intestinalis* settlers had higher survival in the field. Offspring size also determines the outcome of competitive interactions: adults derived from larger offspring are better competitors in the presence of conspecifics (Marshall & Keough 2003b, Marshall et al. 2006). Again, given the benefits of producing larger offspring when intraspecific competition is likely to be high (Marshall et al. 2006), one might expect mothers at higher densities to produce larger offspring. Initial evidence supports this expectation (Allen et al. 2008) but it appears that few published tests are available. Offspring size affects post-metamorphic survival and growth in snails with direct development (Moran & Emlet 2001) and increasing offspring size may also offer a size refuge from predation (Rivest 1983). Whilst it is expected that offspring size effects are likely to be strong in

direct developers, the fact that this group has a mobile juvenile stage (cf. sessile marine invertebrates) makes field tests of more difficult and published studies rare.

Overall, offspring size has pervasive effects throughout marine invertebrate life histories regardless of development mode and for the most part, larger offspring have been shown to have higher fitness (or at least performance) than smaller offspring. Numerous factors such as competition, predation and food abundance can affect the relative benefits of producing large versus small offspring but there are surprisingly few examinations of whether mothers react to changes in the environment in order to optimally provision their offspring. It is suggested that adaptive plasticity regarding offspring size is likely in marine invertebrates but there have been few tests. Nevertheless, whilst adaptive plasticity in offspring size is probably ubiquitous, the magnitude of plasticity is likely to differ across groups. Marshall et al. (in press) compared among- and within-brood variation in offspring size across five phyla of invertebrates. They found that among-brood variation was much higher in direct developers than in species with a larval phase and interpreted this variation as indirect evidence for adaptive plasticity in offspring size in this group (Marshall et al. in press). Because mothers with direct-developing offspring are more able to 'assess' the habitat in which their offspring will be released, it seems likely that this group should exhibit higher levels of adaptive plasticity with regard to offspring size. Furthermore, because direct developers, by definition, do not have a larval stage, the relationship between offspring size and performance is likely to be more direct than in species with a larval stage, enabling mothers to produce offspring of the appropriate size for a particular habitat. In contrast, a species with external fertilisation and a larval stage faces a significant challenge with regard to optimally provisioning its offspring for any single environment. To illustrate, consider the ascidian *Ciona intestinalis*. At high conspecific densities, smaller eggs will be favoured at fertilisation because they are less susceptible to polyspermy (Marshall & Keough 2003c) but producing smaller eggs results in less-dispersive larvae (Marshall & Bolton 2007) that will perform poorly in the presence of conspecifics (Marshall & Keough 2003b). Thus, there are potentially conflicting (and unpredictable) selection pressures acting on offspring size across the life history in species with complex life cycles (Marshall & Keough 2006). Whilst adaptive plasticity is expected in offspring size across a range of development modes in marine invertebrates, it is predicted that this plasticity will be more constrained in species with complex life cycles.

Effects of offspring provisioning on offspring performance: fish   Offspring size effects in marine fishes have received considerable attention from empiricists and theoreticians and a number of excellent reviews have summarised the available literature (Kamler 1992, Chambers & Leggett 1996, Chambers 1997, Heath & Blouw 1998). Therefore, only a brief overview is provided here. The measurement of offspring size effects in fish represents a significant challenge: both the larval and adult stages are usually highly mobile, making it difficult to determine performance measures. As a consequence, fish offspring size effect studies are largely restricted to laboratory conditions and performance measures are typically restricted to early life-history stages. Larval survival and resistance to starvation are the most common measures of performance and, in many species, larvae from larger eggs perform better with regard to both. In a more recent study Grorud-Colvert & Sponaugle (2006) showed that well-provisioned recruits also showed a higher level of predator avoidance behaviour as they did not need to feed as much as poorly provisioned larvae. Despite the initial effects of offspring size being strong, the effects on performance in later life-history stages are less clear.

Some studies have shown that the effects of offspring size diminish over time but confidence in these laboratory-based findings is limited (Heath et al. 1999). The relationship between offspring size and performance is extremely sensitive to local environmental conditions (Kaplan 1992, Einum & Fleming 1999, Fox 2000) and benign laboratory environments can dramatically underestimate

the importance of offspring size effects. Thus, it may be premature to conclude that the effects of offspring size diminish over time in marine fish, particularly given that some excellent studies in freshwater fish have shown reasonably persistent, strong effects on offspring performance (Einum & Fleming 1999, Einum 2003). However, it is worth noting that larger offspring are not always 'better'; in some instances larger offspring suffer higher predation (Kamler 1992, Chambers & Leggett 1996, Chambers 1997, Heath & Blouw 1998, Dibattista et al. 2007). At the very least, it appears that offspring size can affect the early life-history stages of a number of marine fish species and given the importance of recruitment for population dynamics, these effects may be crucial. Given that egg size can affect initial larval growth rate and that larval growth rate can be a good predictor of subsequent post-metamorphic performance in the field (Shima & Findlay 2002), it is suggested that offspring size effects in fish may be stronger than previously thought and generally, larger offspring will have higher fitness than smaller offspring.

Sources of variation in offspring size   Offspring size is an important determinant of subsequent performance in both marine invertebrates and fish, but what are the sources of variation in offspring size? Offspring size is a remarkably plastic trait and can vary according to a range of different factors. This section reviews some common sources of variation in offspring size, examines any common patterns in offspring size variation and attempts to explore if there are any underlying adaptive foundations for these patterns. Offspring size can also vary among populations with factors such as latitude and depth (Sainte-Marie 1991, Bertram & Strathmann 1998, Lardies & Castilla 2001, Kokita 2003). However, studies of these factors are excluded here because it is not possible to rule out genetic differences among these populations rather than non-genetic maternal effects as the source for offspring size variation.

Seasonal variation

Across both marine invertebrates and fish, in species that reproduce throughout the year, mothers produce larger eggs during the cooler winter months and smaller eggs during warmer summer months (Table 1 and Figure 3.3 in Chambers 1997). These changes in offspring size are often associated with a concomitant change in fecundity (see references in Table 1), suggesting that this is an important maternal effect that could change the dynamics of populations across the seasons. In marine invertebrates, the species for which data could be found are largely restricted to copepods and amphipods. This may be due to the fact that these species typically brood their offspring and breed for long periods, making collecting such data relatively straightforward, or these effects may be stronger and more apparent in these groups.

Why do mothers tend to produce larger offspring in the winter months? Table 2 lists the range of factors that can change over the season and all of these factors could affect the size of offspring that are produced, some of which represent direct effects on mothers (i.e., non-adaptive) whilst others could represent anticipatory adjustments of offspring size in order to increase offspring fitness. Whilst each of these factors has the potential to affect offspring size, some have been examined more than others and one of the most popular explanations is that seasonal changes in temperature drive the observed changes in offspring size.

In Chambers's (1997) review of seasonal variation in fish egg sizes, he suggests that temperature regime during oogenesis is the most dominant factor in fish. To support this suggestion, Chambers showed that offspring sizes change irrespective of any factor other than temperature in captive species in controlled conditions. Chambers concluded that the inverse relationship between offspring size and temperature may have no adaptive basis and is more likely to be a simple by-product of a mismatch between the effects of temperature on development and growth (Chambers 1997). Indeed, there is some theoretical support for such an effect and it has been suggested that a decrease in offspring size associated with increased temperature be regarded as a physiological inevitability

Table 1 Summary of studies reporting seasonal changes in offspring size in marine invertebrates

Study	Group	Species	Season or factor associated with size increase	Study type
Sheader (1996)	Amphipoda	*Gammarus insensibilis*	Winter	Field
Soto et al. (2006)		*Ampelisca araucana*	Winter	Field
Jeong et al. (2007)		*Jassa slatteryi*	Autumn (cf. spring)	Field
Yu & Suh (2006)		*Synchelidium trioostegitum*	Autumn (cf. spring)	Field
Pardal et al. (2000)		*Ampithoe valida*	Winter (cf. spring)	Field
Sheader (1983)		*Gammarus duebeni*	Winter	Field
Bell & Fish (1996)		*Pectenogammarus planicrurus*	Winter	Field
Skadsheim (1984)		*Gammarus oceanicus*	Winter	Field
		Chaetogammarus marinus	Winter	Field
		Chaetogammarus stoerensis	Winter	Field
		Gammarus salinus	No change	Field
Skadsheim (1989)		*Gammarus salinus*	Decreased temperature and salinity	Lab.
Pond et al. (1996)	Copepoda	*Calanus helgolandicus*	Winter	Field
Halsband-Lenk et al. (2001)		*Centropages typicus*	Winter	Field
Diaz et al. (2003)		*Euterpina acutifrons*	Winter	Field
Guisande et al. (1996)		*Euterpina acutifrons*	Food	Lab.
Leme (2006)	Decapoda	*Sesarma rectum*	Winter	Field
Sampedro et al. (1997)		*Pisidia longicornis*	Winter (cf. spring)	Field
Oh & Hartnoll (2004)		*Crangon crangon*	Winter	Field
Timofeev & Sklyar (2001)	Euphausiacea	*Thysanoessa raschii*	Increased temperature and salinity	Field
Pecl (2001)	Cephalopoda	*Sepioteuthis australis*	Summer	Field
Marshall & Keough (2008b)	Bryozoa	*Watersipora subtorquata*	Summer	Field

Table 2 Summary of the factors associated with seasonal changes that could affect the size of offspring that are produced

Parameter	Mechanism	Supporting studies
Maternal environment		
Temperature	Kinetics of growth and provisioning	Sheader (1996), van der Have & de Jong (1996), Chambers (1997)
Maternal size	Maternal size–offspring size correlation	Sakai & Harada (2001)
Maternal age	Maternal age–offspring size correlation	Ito (1997)
Offspring environment		
Temperature	Slower development/decreased performance	Fischer et al. (2003)
	Oxygen demands in brood environment	Hendry et al. (2001)
Nutrition	Decreased food availability	Guisande et al. (1996)
Salinity	Decreased offspring performance	Gimenez & Anger (2001)

(van der Have & de Jong 1996). Alternatively, a change in offspring size in response to temperature could be an adaptive response: for species that feed in the plankton, increases in offspring size decrease the length of the planktonic period, potentially countering the effect of temperature

on developmental rate (Vance 1973, Clarke 1992). One aspect of temperature that has received less attention than the above is its effect on oxygen demands of the brood. Given that temperature will increase the oxygen demand of broods (Baynes & Howell 1996) and larger eggs require more oxygen (Strathmann & Chaffee 1984, Moran & Allen 2007), then mothers may have to reduce the size of their eggs when temperatures are higher such that they receive sufficient oxygen. However, it should be noted that larger eggs do not necessarily suffer more than smaller eggs when oxygen levels are low (Einum et al. 2002). Whilst temperature represents a good candidate for the underlying factor for seasonal changes in egg size, whether the change be an adaptive response or not, there are other factors that may play an important role.

In addition to temperature, environmental factors such as food and salinity, and maternal factors such as age and size, and the likely competitive environment of offspring will also change across the season. For example, Guisande et al. (1996) showed that *Euterpina acutifrons* mothers that experience lower food levels (which occur during winter) produce larger offspring. This change in offspring size was viewed as an AME: mothers increase the size of their offspring so that they can better cope with low food conditions. Food levels are typically lower during the winter months and development is slower. So if increased offspring size allows offspring to develop faster or cope with lower food levels, then mothers may gain a fitness benefit from producing larger offspring. Thus, the seasonal pattern in offspring size has been interpreted as an adaptive strategy by which mothers maximise fecundity (by producing smaller eggs) when selection on increased egg size is relaxed during the warmer months (Skadsheim 1984, Bell & Fish 1996). It is particularly interesting that this explanation has been invoked repeatedly in copepods and amphipods, two groups for which mothers brood their offspring and can detect the likely food conditions that their offspring will experience. Whilst this explanation has intuitive appeal, there are too few studies outside of these groups to determine the generality of this effect.

Gimenez & Anger (2001) found that salinity strongly affects egg size, with mothers producing larger eggs at lower salinities in the estuarine crab *Chasmagnathus granulata*. Embryos utilise more resources during development at lower salinities due to the costs of osmoregulation and so mothers may produce larger offspring in order to cope with this change (Gimenez & Anger 2001). In a number of other studies, it is difficult to disentangle the effects of salinity and temperature as both change over the season (Skadsheim 1989, Timofeev & Sklyar 2001).

External environmental factors are not the only changes that occur across seasons that could affect the size of offspring produced: the mothers producing the offspring also change. The size and age of reproductive mothers can both change across the seasons and both can affect offspring size (see below). Whilst some studies have separated maternal size differences from seasonal effects (Soto et al. 2006), it is worth noting that any systematic differences in maternal size/age across seasons may also affect offspring size and should be noted in future studies.

In order to disentangle the competing explanations for seasonal variation in offspring size, two approaches are suggested. First, multifactorial, manipulative studies that vary salinity, temperature and food independently would be useful for determining which factors/cues elicit a change in the size of offspring produced by mothers. Second, measuring the relationship between offspring size and subsequent performance across seasons would be a valuable step for determining whether changes in offspring size across seasons represent an AME by which mothers are maximising their fitness by producing offspring of 'optimal size'. For example, Marshall & Keough (2008b) estimated the relationship between offspring size and performance in the field in summer and winter for the bryozoan *Watersipora subtorquata*. They found that there was a steeper relationship between offspring size and post-metamorphic performance in summer and that this relationship resulted in larger offspring sizes being favoured. These findings matched the observed variation in offspring size across the seasons; the size of *W. subtorquata* larvae was greater in summer than in winter.

Thus, in some instances at least, seasonal changes represent an adaptive response by mothers to maximise their fitness but more studies are needed.

Small-scale temporal variation: maternal age and spawning sequence

As well as showing seasonal variation, offspring size can also vary at smaller temporal scales. The age of mothers can affect the size/quality of offspring they produce. Berkeley et al. (2004) showed that maternal age was an excellent predictor of offspring provisioning and subsequent performance in the rock fish *Sebastes melanops*. Similar effects were suggested for Pacific herring *Clupea pallasii* (Hershberger et al. 2005). For invertebrates, problems associated with accurately aging field-caught individuals make such studies rarer, although Gardner (1997) showed a decrease in offspring size across moults in the crab *Pseudocarcinus gigas*. The size of offspring can also change over a single spawning season but it is unclear whether this is a maternal age effect or not. Jones et al. (1996) found that mothers decreased the size of their eggs over subsequent spawns in the dorid nudibranch *Adalaria proxima*. A similar decrease in offspring size was observed in the annual gastropod *Haloa japonica* (Ito 1997) but interestingly, offspring size increased with maternal body size.

Maternal size

A positive relationship between maternal body size and offspring size is well known in both marine fish and invertebrates. A number of reviews of fish (Chambers & Leggett 1996, Heath & Blouw 1998) provide a comprehensive list of offspring-maternal body size correlations and these lists are not repeated here. In marine invertebrates the relationship appears to be more variable, with many species showing a positive relationship but others show no relationship or even a negative one (Table 3). The underlying causes for this correlation are largely unknown. Sakai & Harada (2001) suggest an intriguing explanation by which larger mothers can provision their offspring more efficiently and quickly than smaller mothers; thus producing larger offspring carries less of a cost for larger mothers relative to smaller mothers. Alternatively, larger mothers may produce larger offspring because they are more fecund and are adaptively provisioning their offspring to deal with higher levels of competition (McGinley et al. 1987). If the relationship between maternal body size and offspring size is an adaptive response to increased sibling competition, the relationship would be expected to be more common in species with philopatric or poorly dispersing offspring. Whereas the compilation of studies considered in the present review is by no means exhaustive (and probably underestimates the number of species for which no relationship occurs), no such size relationship pattern can be found, but further studies that specifically address this intriguing question are awaited. Alternatively, offspring-maternal body size relationships may simply be a product of physiological constraints and have no adaptive basis (Congdon & Gibbons 1987, Fox & Czesak 2000), but this explanation seems to be unlikely for most species.

Maternal nutrition

Maternal nutrition can have mixed effects on offspring size. While some studies show that a decrease in maternal food availability decreases offspring size (Bayne et al. 1978, Qian & Chia 1991, Qian 1994, George 1995, Chester 1996, Krug 1998, Meidel et al. 1999, McCormick 2003, Steer et al. 2004, Gagliano & McCormick 2007), others show an increase in offspring size in response to decreased food availability (Guisande et al. 1996, Allen et al. 2008). This variation in the effects of maternal nutrition is a good example of why such effects need to be viewed in a maternal effects framework. It is suggested that decreases in offspring size represent a SME while increases in offspring size represent an AME (although whether a change in offspring size is viewed as a decrease or an increase depends on the point of reference). Ultimately, whether a decrease in maternal food results in an AME or a SME will depend on (1) whether mothers have an opportunity to reproduce at some later stage and/or (2) whether maternal nutrition is a good predictor of offspring nutrition.

Table 3 Summary of studies investigating the effect of maternal body size on offspring size

Study	Species	Development	Relationship
Invertebrates			
Green (1998)	*Keratella cochlearis*	D	+ve
Miloslavich & Dufresne (1994)	*Buccinum cyaneum*	D	+ve
Ilano et al. (2004)	*Buccinum isaotakii*	D	+ve
Valentinsson (2002)	*Buccinum undatum*	D	—
Kohn & Perron (1994)	*Conus* spp. (13 spp.)	P	No relationship in 11/12 species but –ve in *C. marmoreus*
Chaparro et al. (1999)	*Crepidula dilatata*	D	+ve
Ito (1997)	*Haloa japonica*	L	+ve
Steer et al. (2004)	*Euprymna tasmanica*	D	—
Bridges (1996)	*Capitella* sp. I *(cf. Capitella capitata* Fabricius*)*	P	+ve
McCarthy et al. (2003)	*Phragmatopoma lapidosa*	P	—
Bridges & Heppell (1996)	*Streblospio benedicti*	L	+ve
McLaren (1965)	*Pseudocalanus*	?	+ve
Soto et al. (2006)	*Ampelisca araucana*	B	—
Sheader (1983)	*Gammarus duebeni*	D	—
Dunn & McCabe (1995)	*Gammarus duebeni*	D	+ve
Jeong et al. (2007)	*Jassa slatteryi*	B	+ve
Bell & Fish (1996)	*Pectenogammarus planicrurus*	B	+ve in 1/9 samples
Yu & Suh (2006)	*Synchelidium trioostegitum*	B	+ve
Clarke (1992)	*Ceratoserolis trilobitoides*	B	+ve
	Serolis polita	B	—
Willows (1987)	*Ligia oceanica*	D	+ve
Sampedro et al. (1997)	*Pisidia longicornis*	P	—
Clarke (1993)	*Chorismzis antarcticus*	P	+ve
	Eualus gaimardii	P	+ve
	Nematocarcinus lanceopes	P	+ve
	Notocrangon antarcticus	P	—
Kim & Hong (2004)	*Palaemon gravieri*	P	—
Gimenez & Anger (2001)	*Chasmagnathus granulata*	P	+ve
Dugan et al. (1991)	*Emerita analoga*	P	+ve in 8/22 sites
Damiani (2003)	*Pagurus longicarpus*	P	—
Ouellet & Plante (2004)	*Homarus americanus*	P	+ve
DeMartini & Williams (2001)	*Scyllarides squammosus*	P	—
Barnes & Barnes (1965)	*Semibalanus balanoides*	P	+ve
Marshall et al. (2003), Marshall (2005)	*Bugula neritina*	L	+ve in 2/3 sites, –ve in 1/3
Bingham et al. (2004)	*Leptasterias aequalis*	D	+ve
Marshall & Keough (2003c)	*Uniophora granifera*	L	+ve
Marshall et al. (2000)	*Pyura stolonifera*	L	+ve
Marshall & Keough (2003b)	*Ciona intestinalis*	L	+ve
Fishes			
Bradford & Stephenson (1992)	*Clupea harengus*	P	+ve spring spawners but not autumn spawners
Ware (1985)	*Clupea pallasii*	P	+ve
Ciechomski (1966)	*Engraulis anchoita*	P	+ve

Table 3 (continued)   Summary of studies investigating the effect of maternal body size on offspring size

Study	Species	Development	Relationship
Hinckley (1990)	*Theragra chalcogramma*	P	—
Hislop (1988)	*Melanogrammus aeglefinus*	P	+ve
Marteinsdottir & Able (1988)	*Fundulus heteroclitus*	B	+ve for 1/2 populations
Bengtson et al. (1987)	*Menidia menidia*	P	—
Pankhurst & Conroy (1987)	*Hoplostethus atlanticus*	P	—
Koslow et al. (1995)	*Hoplostethus atlanticus*	P	—
Conroy & Pankhurst (1989)	*Allocyttus niger*	P	—
	Pseudocyttus maculatus	P	—
McEvoy & McEvoy (1991)	*Psetta maxima*	P	+ve
Buckley et al. (1991)	*Pseudopleuronectes americanus*	P	+ve

Note: Relationship is indicated as positive (+ve), negative (–ve), no relationship, or not reported (—). Invertebrate modes of development: B, brooder; D, direct development; L, lecithotrophic larvae; P, planktotrophic larvae. Fish modes of development: B, benthic eggs; P, pelagic eggs.

There appears to be a temptation in the marine literature to view mothers as simple conduits by which environmental variation affects offspring size. However, terrestrial studies illustrate that it is not as simple as 'poor provisioning in, poor provisioning out' and in many instances, mothers can buffer offspring from poor nutritional conditions by increasing the size of their offspring. Similar effects are likely in marine organisms but, in order to observe these effects, there must be a focus on natural variation in maternal nutrition. If maternal nutrition is reduced to unnaturally low levels, then mothers may reduce the size of their offspring but this gives little information about the role of maternal nutrition in determining offspring size because the mother is being presented with a novel nutritional stress. Further studies would be welcome that examine the role of maternal nutrition in determining offspring size, using natural variation in maternal nutrition, but that do not confound population effects with differences in nutrition.

Summary of the sources of offspring size variation

Identifying the underlying causes of offspring size variation is problematic because important life-history traits are often correlated. For example, offspring size could increase in summer months because mothers are responding to changes in the environment their offspring will encounter, because the average size or age of mothers has changed or because mothers have access to more or less food. Disentangling these competing hypotheses will be difficult but ultimately rewarding given that offspring size can have profound effects on the recruitment success and subsequent population dynamics of marine populations. What is clear is that offspring size is a highly dynamic trait under a range of maternal influences and many factors can modify the size of offspring mothers produce.

Brood care

Offspring size/provisioning does not represent the only reproductive investment that mothers can make in their offspring, they can also protect the offspring from predation and maintain local environmental conditions such that they benefit offspring. These behaviours tend to increase offspring fitness at the expense of current or future maternal fecundity and as such, the balance between maternal care and fecundity (from a life-history theory perspective) is determined by the same considerations as those for the balance between offspring size and fecundity. The various aspects

of brood care and how they act as a maternal effect are discussed next. Note that the authors do not consider the simple act of 'brooding' of offspring on/in the body as being a maternal effect, but focus on maternal behaviours that (1) have the potential to affect offspring performance/phenotype and (2) show signs of, or the potential to, vary among individuals of the same species according to the maternal phenotype or environment. Although brood care by fathers is relatively common in marine fish, this type of care is excluded from this review as it is not a maternal effect.

Many species of both invertebrates and fish brood their offspring on their bodies. One of the main constraints to brooding in the marine environment is the low diffusion coefficient and solubility of oxygen, which affects oxygen acquisition and therefore the capacity to aggregate embryos (Fernandez et al. 2003, Green & McCormick 2005, Fernandez et al. 2006b). Accordingly, many brooding mothers show specific behaviours that provide oxygen to embryos to enhance development, survival and growth of the brooded embryos (Wheatly 1981, Chaffee & Strathmann 1984, Strathmann & Strathmann 1995, Naylor et al. 1999). Brooding female crabs adopt very clear behaviours (e.g., abdominal flapping), not present in non-brooding females, which are implicated in both the detection of oxygen conditions and oxygen provision to the embryos (Fernandez et al. 2000, Baeza & Fernandez 2002, Fernandez & Brante 2003). The frequency of abdominal flapping has been found to increase with embryonic development, coinciding with an increase in oxygen demands of the embryos (Baeza & Fernandez 2002). This suggests that brooding females are capable of modifying their behaviour depending on the oxygen demands of their embryos. However, there is a substantial cost associated with active brooding behaviours (Fernandez et al. 2000), which increases with the frequency at which oxygen is provided to the embryos (Baeza & Fernandez 2002), and may increase with body size (Fernandez et al. 2006a).

Brood care can extend beyond the maintenance of oxygen levels for offspring and in some species, mothers appear to carry their offspring for extended periods in order to decrease mortality, which can be high in early juvenile stages. While brood care is not necessarily an obligate reproductive strategy (Thiel 1998a), juveniles receive significant benefits in the form of growth and survival (Aoki 1997, Kobayashi et al. 2002). However, brood care may also lead to conflicts both among offspring and between the mother and offspring, particularly during later life-history stages when resources such as food and space become limiting (Thiel 2003). Furthermore, parasites and other epibionts may be transferred from parents to offspring (Thiel 1998b). The benefits of brood care may be dependent on ecological variables (e.g., presence of predators, Kobayashi et al. 2002), and the duration of brood care is likely to be influenced by the availability of resources such as food and shelter (Thiel 1999, 2003). Maternal care can be particularly costly for species with benthic egg masses that require continual protection as it often results in adults being unable to feed during this period (Bosch & Slattery 1999).

Overall, brood care is likely to represent a significant maternal effect in marine invertebrates and fish with non-dispersive offspring but apart from studies on amphipods (Thiel 1998a, 1999), there are few other examples of how much of an effect brood care has on subsequent offspring performance. This may be because, in many species, brood care is obligate (and therefore, removal of maternal care results in complete reproductive failure) but the suspicion is that even slight variation in the degree of brood care may have profound effects on subsequent offspring performance.

Offspring release

Many life-history studies focus on easily quantifiable maternal effects such as offspring provisioning and offspring phenotype. While these factors can profoundly influence both maternal and offspring fitness, where and when offspring become independent are clearly also important (Resetarits 1996). When environments vary in quality, natural selection should favour mothers that release their offspring in places and at times that increase offspring (or at least, maternal) fitness. This section

first highlights the importance of oviposition 'choices' in the terrestrial literature and then attempts to identify the consequences and prevalence of maternal effects on offspring release in marine organisms. Consideration is then given to the two major ways in which offspring release can affect offspring performance: spatial variation in offspring release and temporal variation in offspring release. Here the terms 'release site' or 'release time' are used to mean the spatial or temporal position where mothers give offspring independence and no longer provide any maternal care. Release site is a general term that can be used when describing all reproductive modes but in this review the term 'oviposition' is used to specifically mean the location where oviparous mothers release their eggs.

Oviposition effects in terrestrial systems

Across many taxa, there is good evidence that mothers select locations to release their offspring based on environmental qualities that increase offspring fitness and this choice can be the "single greatest determinant of offspring success" (Mousseau & Fox 1998b, p. 403). Accordingly, the study of oviposition (the site of egg laying) effects (in insects and amphibians particularly) is a major and sophisticated field (reviewed in Thompson 1988, Thompson & Pellmyr 1991). However, the effect of the location where offspring are released has received less attention in marine systems. To adequately describe the fitness consequences of oviposition across the terrestrial literature is beyond the scope of the present review. A brief list is provided of the different effects that oviposition site can have on offspring phenotype/performance (Table 4), as is a list of the cues mothers use to choose among different potential sites for depositing their offspring (Table 5).

Offspring release site effects in marine systems

In the marine environment, there are some clear potential analogues to the ovipositing phytophageous insects but these marine groups have received relatively little attention. Herbivorous amphipods that are closely associated with marine macroalgae and sacoglossan sea slugs are both groups in which the site of maternal release from brooding (in the case of amphipods) or oviposition (in the case of sea slugs) will strongly affect offspring performance. However, in one of the few studies to consider such effects, Poore & Hill (2006) found no difference in preferences of brooding and non-brooding females, despite performance differing greatly among different host plants (Poore 2004). Nevertheless, it may be expected that in a range of organisms that are closely associated with particular hosts and have poorly dispersing young, the location that offspring are released will have profound consequences for offspring performance.

Species that associate with hosts are not the only marine organisms in which to expect strong effects of oviposition on offspring performance. Von Dassow & Strathmann (2005) found that there was clear ranking of preferences with regard to oviposition sites in the bubble shell snail *Haminaea vesicular*. Mothers preferred to deposit egg masses on red algae and eel grass over other substrata and when more substratum was artificially added, the abundance of snails and egg masses increased, which the authors interpreted as evidence that mothers were limited in their access to suitable sites (von Dassow & Strathmann 2005). It is possible that gastropod mothers that are carrying a high 'egg load' may also show decreases in the stringency of preferences over time as in ovipositing insect mothers but this remains to be tested (Singer et al. 1992). Many other gastropods with benthic egg masses appear to show clear preferences for different substrata and use a variety of cues to identify these substrata and some of these oviposition preferences appear to be related to enhancing offspring survival (Biermann et al. 1992, Benkendorff & Davis 2004). For example, *Neptunea pribiloffensis* lays its eggs next to the sea anemone *Tealia crassicornis*, a behaviour that probably reduces mortality due to grazing by the urchin *Strongylocentrotus droebachiensis* and this laying behaviour has been interpreted as a form of 'babysitting' (Shimek 1981). Importantly, a range of environmental stresses can have profound effects on offspring phenotype, suggesting that any

Table 4 Summary of insect and amphibian studies that report effects of oviposition site on offspring attributes

Effect on offspring	Mechanism	Study
Insects		
Differential survival and growth	Predation/parasitism	Ohsaki & Sato (1994), Loader & Damman (1991)
	Seasonal shift in host availability, seasonal shifts in host nutrient quality that increases age of host leaves that increases sclerophylly in mature leaves	Rausher (1980), Rausher (1981)
Differential survival	Larval size	Rausher & Papaj (1983)
	Egg load	Rausher (1979a)
	Light intensity	Rausher (1979b)
	Intraspecific variation in host quality	Ng (1988)
Differential growth	Food availability	Loader & Damman (1991)
Differential growth	Light intensity (elevated larvae body temperature)	Grossmueller & Lederhouse (1985)
Progeny size	Competing siblings	Rosenheim & Rosen (1991)
Sex ratio	Host body size	Jones (1982), King (1988)
	Temperature	Lysyk (2000)
Host plant preference	Imprinting	Anderson et al. (1995)
Amphibians		
Differential survival	Temperature	Howard (1978)
	Predation	Resetarits & Wilbur (1989)
	Conspecific cannibalism	Spieler & Linsenmair (1997)
	Desiccation	Spieler & Linsenmair (1997)
	Pathogen	Kiesecker & Blaustein (1997)
	Parasite	Kiesecker & Skelly (2000)
	UV-B	Palen et al. (2005)
	Pond size (linked to desiccation probability)	Seale (1982)
Differential growth	Competition	Lawler & Morin (1993)
	Canopy cover/temperature	Skelly et al. (2002)
	Parasite	Kiesecker & Skelly (2000)

differences in oviposition location may be important (Przeslawski 2004). However, what is largely lacking is information on the degree of variation in oviposition preferences among mothers and, most importantly, the consequences of this variation for the subsequent performance of offspring (but see Biermann et al. 1992 for a rare exception).

Variation in oviposition location among broods of eggs is not the only source of maternal effects on offspring survival; location within a brood or clutch may also be important. In acanthosomatid stinkbugs, eggs deposited on the outside of the egg mass suffer higher predation than those on the inside of the egg mass (Kudo 2001). The authors are unaware of any similar studies on predation in marine organisms but there are other effects of the position in the egg mass in marine species. Booth (1995) showed that in the gastropod *Polinices sordidus*, eggs in the middle of the large (37-mm diameter) egg mass had access to less oxygen and developed more slowly than eggs in the outer region of the egg mass. Other gastropod egg masses are constrained by the availability of oxygen (Strathmann & Chaffee 1984) and it is likely that this particular maternal effect (position within the mass) will have important consequences for the timing of offspring emergence and the size/quality of offspring emerging from the egg mass.

The location in which offspring are released for organisms with sedentary offspring or those that produce egg masses is an obvious candidate for a maternal effect but what about species that

Table 5 Summary of insect and amphibian studies that report factors influencing maternal choice on oviposition site

Cue	Ovipositing species	Host	Study
Family of plant	Various lepidopterans	Various species	Ehrlich & Raven (1964)
Plant species	*Papilio machaon*	Various species	Wiklund (1975)
	Various *Heliconius* spp.	Various *Passiflora* spp.	Smiley (1978)
Light intensity	*Battus philenor*, *B. polydamus*, *Parides montezuma*	*Aristolochia orbicularis, A. micrantha*	Rausher (1979b)
	Papilio glaucus	*Prunus serotina*	Grossmueller & Lederhouse (1985)
Plant morphology	*Battus philenor*	*Aristolochia reticulata, A. serpentaria*	Rausher (1978)
Plant density	*Battus philenor*	*Aristolochia reticulata*	Rausher & Papaj (1983)
Plant chemistry	*Pieris rapae*	Cruciferae	Renwick & Radke (1983)
Egg load on plant	*Battus philenor*	*Aristolochia reticulata, A. serpentaria*	Rausher (1979a)
Egg load in mother	*Battus philenor*	*Aristolochia reticulata, A. serpentaria*	Odendaal & Rausher (1990)
Plant nutritional quality	*Battus philenor*	*Aristolochia reticulata, A. serpentaria*	Rausher (1981)
Plant sclerophylly	*Battus philenor*	*Aristolochia reticulata, A. serpentaria*	Rausher (1981)
Maternal experience	*Battus philenor*	*Aristolochia reticulata, A. serpentaria*	Rausher (1978)
	Euphydryas editha	*Castilleja indivisa, Plantaga erecta, Collinsia tinctoria, C. parviflora, C. bicolor*	Singer (1982)
Particular plants in a population	*Euphydryas editha*	*Pedicularis semibarbata*	Ng (1988)
Experience as larvae	*Spodoptera littoralis*	N/A	Anderson et al. (1995)

Note: N/A = not applicable.

release dispersive, planktonic larvae? Evidence for an effect of offspring release location on offspring performance is limited but given that many organisms with planktonic larvae migrate to specific spawning locations or show distinct offspring release behaviours (MacFarlane & Moore 1986, McEuen 1988, Fleming 1996, Kotake et al. 2005, Corgos et al. 2006), this is likely to affect subsequent offspring performance and be an important source of maternal effects. Even if mothers do not migrate to a location to release their offspring, offspring are essentially 'inheriting' the environment in which their mothers occurred. Thus the chances of an offspring performing well or poorly may be strongly affected by the quality of the environment in which the mother occurs and releases her young, a non-genetic maternal effect that has received little attention in either marine or terrestrial systems.

Timing of offspring release

Just as the location in which offspring are released can affect subsequent performance, so can the time at which offspring are released. For example, Searcy & Sponaugle (2000) found seasonal differences in the performance of *Thalassoma bifasciatum* larvae, with spring cohorts spending shorter times in the plankton than autumn cohorts. Similar effects appear to occur in other marine fish (Amara et al. 1994, Marteinsdottir et al. 2000) but specific investigations are rare. In his excellent review of the factors affecting, and consequences of, the timing of larval release, Morgan (1995) suggests that there is a hierarchy of cues that regulate the release of crab larvae. Morgan (1995) suggests that release times are plastic and that there are important fitness consequences for offspring depending on when they are released over both short (diel, tidal) and long (seasonal) temporal scales. The present authors agree and suggest that this is a fruitful line of research because

offspring performance is likely to be as strongly affected by when offspring are released as it is by where they are released.

Mate choice as a maternal effect

The classic view of the sexes is that males compete for fertilisations but females choose males (Bateman 1948). For marine organisms that copulate, transfer spermatophores or pair spawn, females often choose amongst males regarding which individual will fertilise the majority of her eggs (but see Berglund 1991, Berglund et al. 1993 for an interesting exception). Because the maternal environment and phenotype can affect which male is mated with and because offspring performance may in turn depend on male identity, mate choice can be viewed as a maternal effect. To date, the majority of positive associations in marine species between mate preference and offspring survival have been found in reef fish. However, whether this is a true reflection of the prevalence of adaptive mate choice across marine taxa or purely an artefact of the ease of observing and detecting mate choice and its consequences in these species is unclear. Although several studies have found relationships between indicator traits used to select mates and offspring fitness, evidence for 'adaptive' mate choice is highly variable in quality and appears to be quite different between species with demersal and pelagic eggs (Petersen & Warner 2002).

One of the commonest forms of female choice in benthic-spawning fish is to lay eggs in nests already containing eggs (Magnhagen & Kvarnemo 1989, Petersen 1995, Forsgren et al. 1996, Kraak 1996a, Petersen & Warner 2002). This behaviour may be explained by a reduced risk of predation or cannibalism ('the dilution effect'; Petersen & Marchetti 1989, Forsgren et al. 1996), increased parental care (Sargent et al. 1986), or mate-choice copying. Much debate has centred on whether female preference for males with eggs in their nest is an adaptive response to increased egg survival or purely a form of 'copying' (Pruett-Jones 1992, Jamieson 1995, Kraak 1996b). Although these two hypotheses are not mutually exclusive, female preference for nests with an intermediate number of eggs and eggs in earlier stages of development suggests female choice for egg survival rather than mate-choice copying (Cote & Hunte 1989, Hoelzer 1990, Jamieson 1995). Furthermore, in choice trials, females do not always copy the observed mate choice of other females (Forsgren et al. 1996). Regardless, copying may be equally adaptive to independent mate choice if direct male assessment is costly and/or some females are less able to discriminate and choose higher-quality males. Therefore, females' preference for males with eggs in their nest is most likely to be an adaptive maternal effect, resulting in direct benefits via increased offspring survival (Petersen 1995, Forsgren et al. 1996, Kraak 1996a).

Female choice for males already guarding eggs may not always be adaptive as male clutch size does not always influence egg survival. For example, in *Stegastes partitus*, egg survival remained unchanged over the normal range of brood sizes defended by males, most likely because the majority of egg losses occur at night when males are not defending their eggs (Knapp & Kovach 1991). Moreover, significant variation exists among males in the number of eggs cannibalised, probably depending on male condition (Kraak 1996a). Therefore, for mate choice to be adaptive, females must be able to detect such quality differences. Females may base their mate choice on egg presence only when other characters are approximately equal. Alternatively, choice could be based on several cues, taking each into account according to some priority or weighting system.

Before any males have obtained eggs, females may spawn with the largest males defending the best-quality nest sites, or they may spawn randomly among a group of males (Jamieson 1995). Numerous studies have found a female preference for large males (e.g., Thompson 1986, Hastings 1988, Gronell 1989) and a positive correlation between male size and egg survival (Cote & Hunte 1989, Knapp & Warner 1991). In addition, females may be able to vary the number of eggs released during a spawning act, releasing more eggs when spawning with larger males; alternatively females

may choose to spawn with larger males when they have more eggs to lay (Cote & Hunte 1989). Conversely, some studies have failed to find a relationship between male size and egg-hatching success (Knapp & Kovach 1991, Petersen 1995) and consequently no female preference for male size alone (Magnhagen & Kvarnemo 1989, Petersen 1989, Knapp & Kovach 1991, Pampoulie et al. 2001). This lends support to the hypothesis that female choice in benthic-spawning fish is an AME as females are apparently only using male traits that correlate with offspring survival. However, in some cases, although females preferentially spawned with larger males, the proportional survival of egg batches was uncorrelated with male size (Cole & Sadovy 1995).

Overall, mate choice is likely to have strong effects on subsequent offspring performance, particularly in species such as benthic-spawning marine fish. Similar mate choice effects may exist in some other organisms but information is scarce.

Adaptive manipulation of offspring phenotype

There are a number of maternal effects that do not clearly fit into the other categories that have been discussed in this section but nevertheless have the strong potential to affect the performance of offspring. Table 6 summarises non-marine studies that have shown an adaptive manipulation of offspring phenotype in response to environmental stimuli; marine organisms have received less attention. These effects are included in this review, despite the fact that marine examples are rare, because they are equally likely to occur in marine organisms and it is hoped that highlighting them may stimulate research in these areas. Adaptive offspring size variation has been explicitly excluded from this list as this maternal effect is covered elsewhere in this review. For simplicity and brevity, environmental sex determination in marine turtles is excluded from the review; this maternal effect is, however, common in this group. From Table 6, it is clear that there is a range of factors that could affect the phenotype of offspring in the marine environment that have not been explored. However, there are some initial indications that a number of these maternal effects are likely to be common among marine organisms.

The effect of maternal environment on the dispersive properties of offspring observed in lizards and aphids has some clear analogues in marine systems. Krug (1998) showed that when *Alderia modesta* mothers (that previously produced only lecithotrophic larvae) were starved, they produced a higher proportion of dispersive, planktotrophic larvae. Krug (1998) suggested that this change

Table 6 Summary of studies reporting environmental stimuli that can induce the manipulation offspring phenotype by mothers

Maternal effect	Environmental stimulus	Study	Species
Predation resistance	Predator kairomones	Agrawal et al. (1999)	*Daphnia culcullata*
	Herbivory	Agrawal et al. (1999)	*Raphanus raphanistrum*
Pollution resistance	Cadmium	Lin et al. (2000)	*Oreochromis mossambicus*
	Mercury	Vidal & Horne (2003)	*Tubifex tubifex*
Dispersal phenotype	Maternal parasitism	Sorci et al. (1994)	*Lacerta vivipara*
		Massot & Clobert (1995)	*Lacerta vivipara*
	Maternal nutrition/competition	Mousseau & Dingle (1991)	Aphidae
Diapause	Temperature, photoperiod	Reviewed in Mousseau & Dingle (1991)	Many insects
Sex determination	Maternal nutrition	Warner et al. (2007)	*Amphibolurus muricatus*
		Reviewed in Cameron (2004)	Mammalia
Disease resistance	Pathogen exposure	Grindstaff et al. (2006)	*Ficedula hypoleuca*
	Environmental quality	Mitchell & Read (2005)	*Daphnia magna*

in offspring phenotype was an adaptive strategy by which mothers produced offspring that were more likely to escape a poor nutritional environment. Similarly, Marshall (in press) found that when *Bugula neritina* mothers were exposed to a brief pollution stress (copper), they produced larvae that swam for longer than larvae produced by unexposed mothers. Marshall (in press) also found that offspring from pollution-stressed mothers were more resistant to that pollutant themselves. If maternal experience is a good predictor of the likelihood of pollution stress, then mothers may be manipulating the phenotype of their offspring such that they are more likely to escape that stress and be more resistant to exposure themselves.

Maternal experiences of competition may also affect offspring phenotype. Allen et al. (2008) found that *Bugula neritina* colonies that had experienced high levels of competition produced more dispersive offspring than colonies that had not experienced competition. In a rare example in fish, Kerrigan (1997) found that if *Pomacentrus amboinensis* mothers experienced competition, they produced larvae that were longer with larger heads, possibly to increase their ability to resist competition themselves. Overall, it is likely that mothers manipulate the phenotype of their offspring according to local conditions in a range of ways in the marine environment but most of the potential effects on offspring phenotype remain largely unexplored.

Maternal environmental effects

Most of the maternal effects that have been discussed thus far have focused on changes in the offspring phenotype that are largely due to the maternal phenotype. However, there is another type of maternal effect by which the maternally determined environment directly affects the performance of the offspring either before release from the mother or after release. For example, the exposure of amphipod mothers to hypoxic conditions can kill brooded offspring before they are even released from the brood chamber (Wiklund & Sundelin 2001). Thus, regardless of offspring genotype, their performance is affected by the maternal environment. Post-release maternal environment effects are likely to occur in offspring that show low dispersal initially after release from the mother and can take two forms. The first maternal environment effect occurs because offspring essentially 'inherit' the environment of their mothers and so offspring performance will be determined by where they are released. In species with mobile mothers this effect can be mitigated by maternal choice of release location and time as discussed above but for sedentary or sessile organisms, offspring will (at least at first) inherit the environment in which their mothers occurred. The ultimate effect of inheriting the maternal environment will also depend on the degree to which offspring can disperse and the scale of environmental variation. Nevertheless, for some species for which offspring dispersal does not exceed the scale of environmental variation, offspring performance may be strongly influenced by the maternal environment and there may be a (non-genetic) correlation between offspring maternal performance due to this maternal environment effect.

The second maternal environment effect that may occur is through differential female fecundity. Offspring from highly fecund mothers will experience (at least initially) higher sibling competition than offspring from less-fecund mothers. Again, if offspring are highly dispersive, then this effect is probably uncommon but if offspring are likely to encounter/compete with siblings then this will affect their overall performance. Interestingly, McGinley et al. (1987) predict that larger (and thus more fecund) mothers should produce larger offspring than smaller mothers because these offspring are more likely to experience competition and may require more resources. The predictions of McGinley et al. (1987) appear to be supported by Einum & Fleming (2002), who suggest that maternal body size-offspring size correlations are more common in fish with benthic-developing eggs than in fish with pelagic eggs. Competition for resources may not be the only maternally induced environmental effect that offspring may experience. The number of siblings that an offspring is released with (i.e., maternal fecundity) may also affect its chances of being preyed upon (Leslie

2005) and, in benthic egg masses, its oxygen environment (Strathmann & Chaffee 1984, Booth 1995). These ideas have not been explored in marine organisms in depth but it is worth noting that the maternal environment itself is capable of affecting offspring phenotype and maternal fecundity can also be an important determinant of offspring environmental conditions.

Constraints on anticipatory maternal effects

Throughout this review the pervasive nature of maternal effects has been highlighted and the prevalence of maternal effects in other systems emphasised. However, it is not the authors' wish to provide an unbalanced view of maternal effects: maternal effects will not always occur, will certainly not always be adaptive for either offspring or mother and will not always persist. In this section some of the constraints on maternal effects are reviewed, specifically why AMEs may not always occur despite the clear benefits of such effects. First, AMEs will be considered as a form of adaptive (transgenerational) phenotypic plasticity.

There must be constraints on adaptive transgenerational phenotypic plasticity; if there were not, mothers would be able to consistently match the phenotype of their offspring to the environment. The constraints on maternal effects as adaptive phenotypic plasticity across generations are similar to the constraints on adaptive phenotypic plasticity within a generation. The difference between the two is that for AMEs the environmental cue is experienced by the mother and the effect is on the offspring phenotype, whereas for adaptive plasticity the environment of one individual induces a phenotype change in that same individual. DeWitt et al. (1998) classed adaptive plasticity constraints into costs and limitations and, in terms of maternal effects, the costs and limitations may act on the mother, offspring or both. DeWitt et al. (1998) lists nine costs and limitations that may constrain the evolution of adaptive phenotypic plasticity (Table 7) and whilst there has been some debate over this list (van Kleunen & Fischer 2005), it is here regarded as a useful base for considering this issue. Each of these costs and limitations is likely to apply to AMEs and whilst exploring each of these in detail is beyond the scope of this review, what are believed to be the most prevalent and likely in the marine environment are highlighted. These are (1) information acquisition costs, (2) production costs, and (3) information reliability limits.

Information acquisition costs

There are a number of costs associated with mothers acquiring information about the offspring environment so that they can adjust the phenotype of their offspring appropriately. DeWitt et al. (1998) highlight the costs of producing and maintaining sensory structures as a cost based on morphology but the act of gaining information about the habitat of the offspring may also have an associated cost. For example, ovipositing mothers may need to search multiple habitats before releasing their offspring, which is at least energetically expensive and at worst carries some predation risk (Stamps et al. 2005).

Production costs

Some phenotypes are simply too expensive to produce. For example, if competition is extremely high and offspring require massive amounts of resources to survive, mothers may still not increase their per-offspring investment because it would dramatically reduce their fecundity. Overall if the costs of 'rescuing' the phenotype of offspring outweigh the benefits, then AMEs in this situation are unlikely (Bernardo 1996a,b). There is another form of production cost that is particularly relevant to marine organisms with complex life cycles: trade-offs among life-history stages. In this review we noted the example of *Ciona intestinalis*, for which larger offspring were favoured in one life-history stage but smaller offspring were favoured in another (Marshall & Keough 2003b,c, Marshall & Bolton 2007). In frogs, for example, a predator-resistant larval phenotype results in a

Table 7 Modified table from DeWitt et al. (1998) summarising the potential costs and limitations of transgenerational phenotypic plasticity

Costs	
Maintenance costs	Costs of producing and maintaining structures used to sense and predict offspring environment, incurred by mothers
Production costs	Costs of producing the desired phenotype, incurred by mothers (e.g., provisioning offspring to increase offspring size) or by offspring (mother induces a response for the offspring to change phenotype, e.g., grow spines in response to predation)
Information acquisition costs	Costs of acquiring information about the environment the offspring will experience (e.g., risk of predation to mothers, energetic cost of search behaviour in oviposition)
Developmental instability	Increased plasticity may result in increased developmental problems (e.g., functional asymmetry)
Genetic costs	Pleiotropic effects of having a plastic phenotype whereby more plastic genotypes perform poorly in stable conditions
Limitations	
Information reliability limit	Mothers limited in their ability to predict the environment when an environmental cue (information) is not present or is unreliable
Lag-time limit	Offspring phenotype must be expressed within a certain time from when the mother experiences the cue; transgenerational plasticity can be limited if the environment changes before the offspring's phenotype can be expressed or the phenotype is not expressed fast enough
Developmental range limit	Plasticity may not be able to produce extreme offspring phenotypes in extreme environments; non-plastic offspring phenotypes may be better suited to those extreme environments and have higher fitness over plastic phenotypes, in such environments non-plastic offspring are favoured and plasticity is limited
Epiphenotype limit	When offspring phenotypes are 'added' onto existing phenotypes, they are termed epiphenotypes; if these epiphenotypes are weaker than phenotypes induced during early development, then plasticity is limited

lower-quality adult phenotype (Relyea 2000, 2001). Thus selection on the entire life history will determine whether transgenerational plasticity carries a survival advantage or not.

Information reliability limits

If there is no cue to the likely environment of the offspring, then it is impossible for mothers to adaptively adjust the phenotype of their offspring. A lack of a reliable cue could be due to the maternal environment and offspring environment being displaced in space or time. If offspring initially disperse at a scale that exceeds the scale of environmental variation, then mothers will be unable to adjust the phenotype of their offspring accordingly. Similarly, if the environment varies unpredictably over short timescales, then mothers will be unable to produce offspring of the appropriate phenotype. Such limitations are likely to occur in marine organisms with highly dispersive larval stages and initial evidence supports this finding. Marshall et al. (in press) found that marine invertebrate species with non-dispersing offspring show greater variation in offspring phenotype (size) among mothers than species with dispersing offspring. They also found that there was more variation within individual broods in species with dispersing offspring, suggesting that in these species, mothers are using diversified bet hedging to cope with uncertainty regarding the likely habitat of their offspring (Marshall et al. in press). More generally, it is predicted that AMEs will be found to be more common in marine organisms with less-dispersive offspring relative to species that produce larvae that disperse to other habitats. Note that this does not necessarily preclude species with larval stages from expressing AMEs. For example, species of copepod release larvae in the water column but these larvae are likely to exist in the same habitat as the mother as the scale

of environmental variation in this environment probably does not exceed the scale of dispersal and AMEs have been shown in this group (Guisande et al. 1996).

Other constraints on maternal effects

There has been long-standing and vigorous debate regarding who has 'control' over offspring phenotypes and particularly maternal care (Trivers 1974, Godfray 1995, Livnat et al. 2005). Whilst parent-offspring conflict probably occurs in marine organisms, the authors can find few examples of offspring having 'control' over their own phenotype and many of the studies discussed in this review strongly suggest that mothers determine offspring phenotype. One potential example is that of the diminutive seastar *Parvulustra parvivipara*. This species broods its offspring in brood chambers where sibling cannibalism occurs and fully formed juveniles that are a quarter of her size can emerge from the mother (Byrne et al. 2003, Byrne 2006). In this instance, mothers may be unable to control the size of her offspring such that offspring may emerge that are larger than what would maximise her fitness. Nevertheless, it is suspected that parent-offspring conflict will be rare with regard to the types of maternal effects discussed in this review but it is noted that such conflict can act as a constraint on maternal effects generally.

Physiological constraints will also constrain maternal effects, particularly regarding offspring size. In some species, the optimum offspring size may simply be too large for mothers to produce (due to morphological constraints; e.g., Congdon & Gibbons 1987) or too large for oxygen diffusion to work effectively. Thus the optimum phenotype for mothers to produce may be inaccessible and mothers may produce offspring with a suboptimal phenotype.

The importance of maternal effects in marine systems

Whilst maternal effects are important in any system, there are a number of specific elements of maternal effects that make them of particular interest in marine systems. In this section, the theoretical considerations of maternal effects are first reviewed and then the importance of maternal effects in the marine environment is considered from both an ecological and an evolutionary perspective.

Theoretical considerations

Maternal effects can affect a number of crucial traits in offspring, the effects of which have been considered in theoretical studies. Whilst few theoretical studies have examined marine organisms specifically, there is a range of general maternal effects models that are worth considering. Elkin & Marshall (2007), Fowler (2005), and Stamps (2006) explore the role of maternal effects in the dispersal and habitat selection of offspring. Fowler (2005) demonstrated that maternal effects could have a stabilising effect on (otherwise chaotic) population dynamics. Furthermore, it appears that the presence of maternal effects on populations can result in population cycles or oscillations over the scale of four populations or longer. A similar cyclic effect of maternal effects of population dynamics has been suggested by Ginzburg (1998) but this model did not examine maternal effects on dispersal specifically. Stamps (2006) presented an interesting modification of an earlier model (Stamps et al. 2005) showing that dispersers that receive more energetic reserves from their mothers are more likely to settle in higher-quality habitat. Elkin & Marshall (2007) specifically examine the effect of offspring provisioning on dispersal in marine invertebrates and show that when there are large differences in habitat quality, offspring that have more reserves are more likely to settle in higher-quality habitats than offspring with fewer reserves.

Whilst some models have suggested that maternal effects will have a stabilising effect on population dynamics, there is no clear consensus with many other models suggesting that maternal effects will actually have a destabilising effect (reviewed in Plaistow et al. 2006). This is because maternal

effects can introduce a 'delayed density-dependence' by which there is a time lag between an environmental change (e.g., a decrease in carrying capacity) and a population response (e.g., Rossiter 1994, Lindstrom & Kokko 2002). Whilst the role of maternal effects in decreasing or increasing population stability remains unclear, what is certain is that maternal effects can act as a powerful force linking events in one generation to the population dynamics of the next. Overall, maternal effects are likely to phenotypically link generations in the marine environment but this idea has received little attention in the marine environment. This is remarkable given that links among generations may also constitute links among populations and this idea is discussed further below.

Ecological perspective

Maternal effects, sublethal effects and the production of recruits

In marine systems, the production of recruits in any single population is largely viewed as a product of the number of reproductive adults and their average reproductive success. The existence of maternal effects, particularly the effect of offspring size/quality, suggests that other factors such as environmental quality should also be considered. Obviously, environmental factors will affect the number and fecundity of adults but there is also the potential for more subtle effects on offspring quality. For example, any decrease in the availability of food may not only reduce fecundity, it may also reduce the size of offspring that are produced. Because smaller offspring are likely to have a lower chance of surviving, a decrease in food availability may dramatically reduce future recruitment through the combined effects of decreased offspring quantity and quality.

The impact of sublethal effects on population dynamics is only just being recognised. Sublethal effects such as competition and injury from predation can have subtle effects on the production of offspring and, more importantly, the size/quality of offspring (Bernardo & Agosta 2005). Whilst these effects have received little attention in marine systems, it is likely that there are a range of biological interactions that result in a reduction in the quality of offspring produced by mothers in that population. Overall, it is emphasised that reductions in fecundity are not the single factor related to the production of recruits in marine systems. Rather, maternal effects constitute a link between the maternal environment, the maternal generation and the offspring generation, which creates the possibility for a range of environmental factors to have cascading and potentially dramatic effects.

Marine populations: demographically open but phenotypically closed?

Most marine organisms have a dispersive larval stage that can travel among populations. Traditionally, marine populations have been viewed as demographically 'open,' by which larvae disperse among populations and the population dynamics of any single population is not determined solely by the local production of recruits (Underwood & Fairweather 1989, Caley et al. 1996, Underwood & Keough 2001). More recently, this view has been challenged: studies of reef fish and mussels suggest that marine populations may not be as open as previously thought, with up to 60% of recruits locally derived from the same population (Jones et al. 1999, Swearer et al. 1999, Becker et al. 2007). It is likely that for any single population, some recruits will be locally derived and others will be from other populations but generally speaking, species with longer larval planktonic periods will probably have lower rates of self-recruitment than species with shorter planktonic periods (Shanks et al. 2003). Regardless of the relative levels of self-recruitment, the dynamics of any single marine population will rarely be completely independent from the input of recruits from other populations and overall, most marine populations are viewed as being somewhat demographically linked. However, little attention has been paid to whether marine populations are linked *phenotypically*.

In demographically open marine systems, events in one population can affect the population dynamics through changes in the production and transport of larvae (Caley et a1. 1996). At its most extreme, some populations can act as sources for larvae whilst others can act as sinks by which

there is no net production of recruits in that population and these dynamics have interesting implications for the management of marine populations (Crowder et al. 2000, Armsworth 2002, Figueira & Crowder 2006). While it is now recognised that populations are not demographically independent, populations are typically viewed as phenotypically independent. An implicit assumption of most marine meta-population theories is that the mean phenotype within any single population is independent of the average phenotype of other populations. However, the existence of maternal effects suggests that this assumption may not be appropriate. Consider an environmental stress that affects Population A and changes the mean phenotype of reproductive mothers in this population. This change in maternal phenotype then translates (via a maternal effect) into a change in the mean phenotype of the offspring produced in Population A. If these offspring then disperse and successfully recruit into Population B, then the mean phenotype of Population B will change despite no environmental change occurring in this population. Of course, this assumes that the scale of larval dispersal exceeds the scale of the environment stress. Nevertheless, the existence of maternal effects suggests that marine populations may be 'phenotypically open', by which changes in phenotype in one population lead to changes in phenotype in another population independent of the initial stimulus (Figure 2). This maternal effect-mediated link between the phenotype of settling larvae and their source population environment has some interesting implications for connectivity in the marine environment.

In the marine environment, different populations of the same species can show remarkable differences in their average phenotypes (Keough & Chernoff 1987, Yamada 1989, Bertness & Gaines 1993, Warner 1997, Wright et al. 2000). Warner (1997) speculates that population-level differentiation is due in part to phenotypic plasticity and in part to local genetic differentiation. The present authors agree but suggest that there is another element that is not being considered: maternal effects. Throughout this review instances for which mothers adaptively manipulate the phenotype (e.g., offspring size, pollution resistance) of their offspring have been highlighted. Obviously different phenotypes will be better suited to different conditions and so one could imagine an instance when mothers in one population produce offspring that have the 'best' phenotype for that local population but that phenotype performs poorly in other locations. If so, then externally derived settling larvae may have a lower chance of surviving and recruiting into another population because their mothers have given them the 'wrong' phenotype. Thus maternal effects may act to reduce connectivity
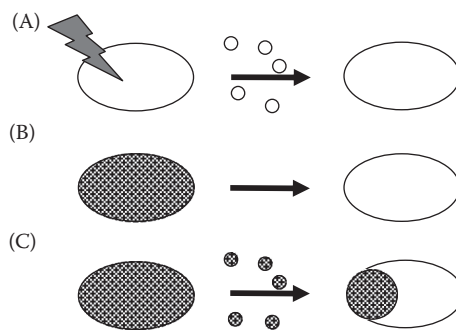

Figure 2 Schematic showing potential role of maternal effects in linking phenotypes between populations. In panel (A), two populations with the same average phenotype (indicated by the open ellipses) and propagules (with the same phenotype) dispersing from the population on the left. An environmental stress occurs in the population on the left and in panel (B), the mean phenotype of the left population changes in response to the stress (indicated by shading). In panel (C), the mean phenotype of offspring dispersing to the population on the right has changed (via maternal effects) and the mean phenotype of the population on the right has been modified (as indicated by shading).
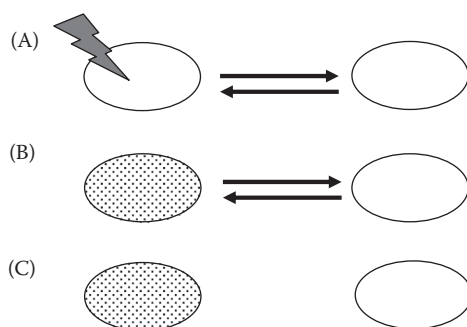
Figure 3 Schematic showing potential role of maternal effects in decreasing connectivity between populations. In panel (A) the populations share the same phenotype and are well linked demographically (indicated by arrows) but an environmental stress occurs in the population on the left. In panel (B) the mean phenotype of the population on the left has changed in response to the stress and thus so has phenotype of the propagules (due to maternal effects). In panel (C) the demographic links among the populations have disappeared because the phenotypes of the exogenous propagules are poorly matched to the local environment.

among marine populations because they result in a 'mismatch' in phenotypes among environments, biasing recruitment success in favour of local recruits (Figure 3).

There are two scenarios by which maternal effects (and thus phenotypic links among populations) can alter marine populations: changes in mean phenotype in one population due to recruitment from another population and decreased connectivity due to a phenotypic mismatch among populations. The relative likelihood of each of these effects will ultimately depend on the proportion of propagules exchanged between populations and the costs and benefits of maternally induced phenotypes across different environments. If the maternally induced phenotype does reasonably well in both populations (e.g., increased offspring size), then maternal effects are unlikely to reduce connectivity. However if, for example, mothers produce offspring that are pollution resistant but are poor competitors in the absence of pollution (Marshall in press), then these offspring are unlikely to successfully recruit into pollution-free populations.

Implications for fisheries management

Many marine fisheries are under intense fishing pressure and most major exploited fish populations have dramatically declined (Hutchings & Reynolds 2004). Furthermore, many fisheries are remarkably slow to recover once exploitation has ceased (Hutchings 2000). Maternal effects may be implicated in the collapse and failure to recover of marine fisheries. As noted in this review, larger, older mothers produce higher-quality offspring that have a great chance of surviving. Many fisheries selectively remove larger fish and decreases in the mean size of exploited stocks are common (Swain et al. 2007). Furthermore, changes in the mean size of reproductive females can be associated with (and possibly precipitate) fisheries collapses (Olsen et al. 2004). These lines of evidence strongly suggest that the effective contribution of older, larger fish to the next generation of recruits is far greater than previously recognised and this maternal effect could play a significant role in the recruitment of exploited stocks (Berkeley et al. 2004). Ignoring this maternal effect and the impact of size-biased fishing could be responsible for a number of fisheries collapses and some have recommended that larger fish be protected on this basis (Birkeland & Dayton 2005). In contrast to this recommendation, some models suggest that maternal age effects on offspring quality will not have major effects on the effects of size-based exploitation (O'Farrell & Botsford 2006). The present authors believe it is likely that larger mothers produce offspring that have far greater chances of survival (either due to producing higher-quality offspring or spawning in higher-quality sites, and

the like) and future fisheries management strategies should incorporate age-/size-based maternal effects.

Implications for aquaculture

The importance of maternal effects for terrestrial agriculture has long been recognised and a similar realisation has begun in aquaculture (Cruz & Ibarra 1997, Deng et al. 2005, Eriksen et al. 2006). As described throughout this review maternal phenotype (often referred to as 'condition' in aquaculture studies) can dramatically affect the survival and performance of offspring and has the potential to dramatically affect yields in aquaculture breeding programmes. However, the relationship between maternal condition and progeny quality is again unlikely to be a simple 'high-quality food in → high-quality offspring out' situation. When conditions are benign, mothers can benefit from producing smaller (lower-quality) offspring and gaining a fecundity benefit (Brockelman 1975). Thus aquaculturists may inadvertently be creating conditions that result in a decrease in the quality of offspring that are produced. Initial evidence in freshwater systems suggest that this can happen (Heath et al. 2003). Clearly, the maternal environment will determine the quality of offspring that are produced and it is predicted that the study of maternal effects will become increasingly important in aquaculture.

Evolutionary perspective

Do maternal effects retard or facilitate species' range expansions?

In the preceding section there was discussion of the potential for maternal effects to reduce population connectivity when different environments stimulate mismatched phenotypes among populations. Such an effect would tend to reduce the probability of a species expanding its range as it is possible that a mother at the edge of the species range will produce an offspring with the 'wrong' phenotype for beyond that range. There is another mechanism by which maternal effects may retard species' range expansions. If the quality of habitat decreases as one moves from the centre of a population to the edge, then mothers may have fewer resources with which to provision their offspring at the edge of the range. If offspring provisioning affects recruitment success (which is likely) then this may result in fewer successful recruits being produced at the edge of the species range and thus reducing the rate of expansion.

Whilst it is argued above that maternal effects can retard species' range expansions, maternal effects could alternatively play a role in expanding species' ranges, particularly regarding invasion by exotic species. Buckley et al. (2003) found invasive populations of Scotch broom, *Cytisus scoparius*, produced larger seeds than native populations and speculated that this could have facilitated the invasion of this species. Einum & Fleming (2004) argue that when environmental conditions are uncertain, mothers should produce larger offspring than usual to ensure survival regardless of local conditions. It may be that the maternal effect of increased offspring size allows invasive marine species to colonise new habitats successfully but this has not been tested as far as the present authors are aware. An intriguing study would be to examine the size of offspring in native and invasive populations of a marine organism and determine whether the patterns shown by Buckley et al. (2003) also occur in the marine environment. Overall, the role of maternal effects in species' range expansions depends on whether the maternal effect is an AME or a SME; the former will facilitate the expansion, the latter will retard the expansion.

Evolution of pollution resistance

Many marine organisms associated with anthropogenic habitats show increased resistance to anthropogenic pollution (e.g., Hoare et al. 1995, Martinez & Levinton 1996, Wallace et al. 1998, Levinton et al. 2003, Mouneyrac et al. 2003, Daka & Hawkins 2004, Rainbow et al. 2004, Piola & Johnston

2006). A strong maternal effect for pollution resistance has been demonstrated for a number of aquatic species for which exposure to a pollutant in the maternal generation increases pollution resistance in the subsequent generation (Munkittrick & Dixon 1988, 1989, Lin et al. 2000, Vidal & Horne 2003, Marshall in press). The role of transgenerational phenotypic plasticity in the genetic evolution of traits remains unclear (Price et al. 2003) but it is possible that the maternal effect of pollution resistance facilitates the genetic evolution of pollution resistance in the sea. Studies that examine the relative role of genetic evolution and maternal effects in determining the resistance of marine populations to pollution would be welcomed.

New approaches and directions

The need for more studies on maternal effects in the marine environment generally has been identified but in this section the emphasis is on some species approaches and directions that may be valuable for investigating maternal effects.

Quantitative genetics approaches

Quantitative genetics approaches have long been used to partition variation associated with maternal effects and describe variation in traits due to additive genetic variance (Falconer 1981). Thus, these approaches can be invaluable for estimating the importance of maternal effects relative to other influences (Heath & Blouw 1998, Heath et al. 1999) but they have been underutilised in marine studies. This is despite the fact that many marine organisms are broadcast spawners, which allows the use of quantitative genetics designs typically only available to those studying plants. Because sperm and eggs from multiple individuals can be crossed in many combinations in broadcast spawners, diallel and 'North Carolina II' designs can be used to examine maternal effects (Lynch & Walsh 1998). Such designs have been used successfully to examine a range of traits in marine broadcast spawners, particularly in aquaculture studies (Boudry et al. 2002, Deng et al. 2005, Evans & Marshall 2005, Marshall & Evans 2005, Ivy 2007) and these powerful tools could be used more frequently for examining maternal effects in the sea.

Marine algae

Throughout this review the focus has been on marine fish and invertebrates and marine algae have largely been ignored. This was not a deliberate strategy; examples of maternal effects in this major and important group were not found. The authors suspect that maternal effects are as prevalent and important in marine algae as other groups and believe that this would be a fruitful line of research, particularly given that there are indications that release time and recruit size can affect a number of key performance traits in this group (Santelices et al. 2003)

Paternal effects

Throughout this review the focus has been on maternal effects, but associated literature searches have yielded some very interesting (non-genetic) paternal effects on offspring performance. In fish particularly, fathers can have strong effects on a number of key offspring traits and paternal brood care, cannibalism and selection/defence of the nesting site are all very important determinants of offspring success (Knapp & Kovach 1991, Payne et al. 2002, Karino & Arai 2006). Obviously, there are also strong paternal effects on offspring performance in sex role-reversed pipefish (Berglund et al. 1986, 1997, Berglund & Rosenqvist 2001). Whilst such effects are less likely in species

without brood care there are a number of other paternal effects that have gone largely untested in marine organisms despite some remarkable effects being documented in other groups. For example, Galloway (2001a) found that the paternal environment affected the properties of offspring in the plant *Campanula americana*. Whether similar effects exist in marine organisms remains largely untested: there may be some surprising paternal effects in the sea.

In most organisms, mothers determine the size of offspring that are produced and in the sea this also holds to a certain extent. However, in marine broadcast spawners, the chances of an egg being fertilised depends on its size because larger eggs are larger targets for sperm (Levitan 1996b, Marshall et al. 2000, 2002). Thus at low sperm concentrations larger eggs are more likely to be fertilised than smaller eggs and at high sperm concentrations, smaller eggs are less likely to suffer lethal polyspermy (Marshall et al. 2002, 2004). This suggests that although mothers may determine the range of zygote sizes that can be produced, males (or more specifically, the amount of sperm that they release) will determine the final size of zygotes that are successfully fertilised. This suggests that in marine broadcast spawners, the paternal (sperm) environment can change the size distribution of offspring produced in the field, a paternal effect that is probably unique to this group.

Conclusion

The present review has shown that maternal effects can act in a variety of ways to strongly influence the subsequent performance of offspring in the marine environment. However, it is recognised that research on maternal effects in marine organisms has only just begun and their importance is only beginning to be appreciated. This review forms only a first glance and summary of the field of maternal effects in the marine environment. The authors anticipate that as interest in these effects grows and matches that for maternal effects research in terrestrial systems, each of the broad types of maternal effects addressed here will become its own subdiscipline and that a broad review such as this will not be possible. The authors look forward to further research in this field and hope that this review proves to be valuable for those interested in maternal effects in the sea.

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